

Behavioural consistency in lizards: links with individual traits and environmental variables

PhD Thesis

By: Gergely Horváth

Supervisor:

Dr. Gábor Herczeg, PhD

ELTE PhD school of Biology

Head of school: Anna Erdei, DSc

Zootaxonomy, animal ecology, hidrobiology Programme

Programme Leader: János Török, DSc



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Introduction

The adaptive value of phenotypic differences within a single population is well accepted since the middle of the 20th century (Wilson, 1998). However, individual behavioural differences were often interpreted as random variation and/or measurement error around an adaptive behavioural mean (Réale et al., 2007), and biological significance of these differences got widely accepted only recently. The term *animal personality* refers to between-individual behavioural differences, which are consistent over time and across contexts (see Gosling, 2001; Réale et al., 2007).

Statistically, animal personality is interpreted as repeatability in a single behavioural trait. In addition to single trait repeatability, between-individual correlations across functionally distinct behaviours (e.g. activity and risk-taking) can also emerge, known as *behavioural syndromes* (Bell & Sih, 2007). Despite the proven behavioural consistency both within and across behaviours, one of the current outcomes in behavioural studies is the recognition of the evolutionary significance of the within-individual component of behavioural variation. The concept of animal personality would suggest that *behavioural plasticity* is highly constrained or even absent, however, data show that even consistent individuals preserves the ability to adjust their behaviour to changing environmental conditions (see Dingemanse & Wolf, 2013). In addition, within-individual behaviour could change independently of environment. These short-term fluctuations are known as *behavioural predictability* in the literature (see Stamps et al., 2012). Growing number of studies claim that behavioural plasticity and predictability are potentially independent components of animal personality *sensu lato*, however, our understanding regarding the evolutionary ecology of within-individual behavioural variance is still incomplete.

The main goal of personality research is to understand the origin of behavioural consistency and identify the mechanisms responsible for its evolutionary maintenance (Bell & Sih, 2007; Sih et al., 2004; Westneat et al., 2015). Accumulating body of evidence suggests that behavioural consistency is linked to individual state- and environmental differences through feedback mechanisms (Sih et al., 2015). Importance of such differences during early stages of ontogeny is well documented (Urszán et al., 2015; Lichtenstein et al., 2016), however, it is still an unresolved question whether environment- and state-based variation influences the strength of behavioural consistency during adulthood and whether the strength of behavioural consistency can change during relatively short periods.

Aims

I aimed to study the determinants of behavioural consistency and different components of individual behaviour in adult animals. I studied state- and environment dependence of behaviour using adult males of two European lacertids as models: The European green lizard (*Lacerta viridis*) and Carpetane rock lizard (*Iberolacerta cyreni*). These species are intensively studied, their biology is well known and they have several traits with described links to individual state and fitness. In particular, my main goals were: (i) to reveal which individual traits are linked to behavioural type (individual mean behaviour) and behavioural predictability in wild-caught adult male lizards and (ii) to test whether short term manipulation of relevant environmental factors would affect behavioural consistency (presence/absence/strength of animal personality and behavioural syndrome) and individual behavioural strategy (behavioural type and behavioural predictability) in wild-caught adult male lizards. As reptiles are rather neglected in personality studies, my thesis is also important to provide data about the behavioural consistency in this vertebrate taxon. The main questions of my thesis were the following:

1. Are animal personality and behavioural syndrome present in adult *L. viridis* and *I. cyreni*?
Is animal personality and/or behavioural syndrome linked to potentially individual state-related variables?
2. Are there any detectable differences between adult and juvenile *L. viridis*' behavioural consistency?
3. Does short-term environmental differences affect the behaviour of adult *L. viridis* and *I. cyreni* at the group (presence/absence/strength of behavioural consistency) and at the individual level (behavioural type and behavioural predictability)?

Materials and methods

I conducted one correlative and one manipulative study on both species. *L. viridis* males were noosed from a population near Tápiószentmárton, Hungary. Animals were transported to the temperature controlled room of the ELTE, where they got housed individually in plastic boxes. I caught *I. cyreni* males at the Puerto de Navacerrada pass (Sierra de Guadarrama mts., Madrid province, Spain). After collection, I transported animals to the ‘El Ventorrillo’ field station, where they got housed individually under semi-natural conditions. I measured the potentially state-linked variables in both species (e.g. size, colouration, rate of parasite infection). Behavioural tests were carried out after a short acclimation period, behaviour of the animals (activity, risk-taking) were measured repeatedly, on consecutive days. Activity was represented by moved distance during one hour, while risk taking was represented by latency to emerge from a refuge after a simulated predator attack.

With the correlative studies, I aimed to detect the presence of animal personality and behavioural syndromes and to test the link between behavioural type and state-variables. In the case of *L. viridis*, I used adult males and their 2-3 weeks old lab-born offspring to test the effect of age on the emergence of behavioural consistency and to estimate the heritability of behavioural type. With the manipulative studies I aimed to test how short-term environmental differences affect different components of behavioural consistency. I applied full factorial designs, however, treatments differed between the species: high vs. low food and long basking time vs. short basking time were applied for *L. viridis*, while high vs. low food and vitamin D₃ supplementation vs. placebo for *I. cyreni*.

To estimate repeatability (animal personality) and between-individual correlations (behavioural syndrome) I applied linear mixed models (LMMs) and bivariate mixed models (BMMs). To test the effect of state variables and environmental differences on behavioural consistency I used general linear models (GLMs), linear mixed models and generalized linear mixed models (GLMMs).

Theses

Correlative studies

1. Behaviour of *L. viridis* and *I. cyreni* males showed significant repeatability, however, there was no sign of behavioural syndromes in *I. cyreni*. This result is in line with the growing number of studies suggesting that behavioural consistency across behaviours (behavioural syndrome) do not necessarily follow behavioural consistency within behaviours (animal personality).
2. Behaviour of adult and juvenile *L. viridis* was repeatable, suggesting that animal personality is rather 'inbuilt' in this species from hatching.
3. Personality of juvenile *L. viridis*' behaviour was 'stronger' than that of the adults'; however, phenotypic behavioural correlation (indicator of behavioural syndrome) was only present in adult males. This result suggests that strength of behavioural consistency is affected by age.
4. I found links between behavioural type and various state variables in adults of both species. On the other hand, there was no correlation between behavioural type and state variables in juvenile *L. viridis*, suggesting that such links are mainly established during ontogeny.
5. Although behavioural type of *L. viridis* families differed significantly, according to father-offspring regression behavioural type is not heritable. However, since the method's assumption, similar age and state of the parental and offspring generation was violated, this result can only be interpreted as providing no support for strong, age- and environment-independent genetic determination.

Manipulative studies

6. Treatment-group-specific repeatability estimates of activity and risk-taking are widely overlapped with that of the pooled sample in both species. This indicates that lowered environmental variation does not necessarily result in lowered consistency.
7. Risk-taking was affected by environment in both species. In the case of *L. viridis*, repeatability was present in all but the optimal treatment group, while the pattern was the

opposite for *I. cyreni*. Moreover, in *L. viridis*, behavioural syndrome was only present in one of the treatment groups. These results indicate that the emergence/maintenance of behavioural consistency is affected by short-term environmental differences.

8. Treatments affected behavioural type of *I. cyreni* but not of *L. viridis*. Treatments also affected behavioural predictability of *L. viridis*. These results suggest that behavioural predictability is a potentially independent component of the individual behavioural strategy.

Conclusions

One of the most important results of my thesis is that short term differences in individual state and environmental conditions are indeed affect the presence and strength of behavioural consistency in adult animals. Moreover, different components of behavioural consistency are affected by short-term environmental variation. The environment-dependence of adult personality is a highly current topic, but unfortunately, studies are scarce and results are rather controversial (DiRienzo et al., 2015; Urszán et al., 2015; Lichtenstein et al., 2016). The fact that under certain circumstances behavioural consistency (consistent between-individual variation) can quickly fade has serious evolutionary consequences, since selection, irrespective of its strength, can only operate of existing between-individual phenotypic variation.

Here, considering the ecological context (the short and synchronized mating season), the patterns are biologically significant, but cannot be interpreted on long term. Longitudinal studies would be necessary to reveal the changes on behavioural consistency on long-term, especially as my own results indicate that age may not just affect the emergence and strength of behavioural consistency, but the link between animal personality and state as well. In addition, long-term studies are important to detect whether state- and environmental variables are affect behavioural consistencies through positive or negative feedbacks. Nevertheless, as the biological role of the applied treatments can be seen general, broad conclusions regarding the emergence and evolution of behavioural consistency can be drawn.

My results support the notion that behavioural predictability is affected by state and environmental differences (Biro & Adriaenssens, 2013; Briffa, 2013). However, it is important to note that behavioural consistency does not necessarily reduce behavioural plasticity, which is another, potentially independent component of within-individual behavioural variation. As our understanding regarding the mechanisms affecting emergence and evolution of behavioural

plasticity and predictability is still poor, joint investigation of different within-individual behavioural variation components would be necessary.

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Publications that are parts of the thesis

- Horváth, G.**, Mészáros, B., Urszán, T.J., Bajer, K., Molnár, O., Herczeg, G. Environment-dependence of behavioural consistency in adult male European green lizards (*Lacerta viridis*). *PLoS ONE* (under review)
- Horváth, G.**, Martín, J., López, P., Garamszegi, L. Z., Herczeg, G., 2017. Food and vitamin D₃ availability affects lizard personalities: an experiment *Behavioral Ecology and Sociobiology*. 71, 27, doi: 10.1007/s00265-016-2257-1
- Horváth, G.**, Martín, J., López, P., Garamszegi, L. Z., Herczeg, G., 2016 Blood parasite infection intensity covaries with risk-taking personality in male Carpetan rock lizards (*Iberolacerta cyreni*). *Ethology*. 122, 355-363, doi: 10.1111/eth.12475
- Bajer, K.*, **Horváth, G.***, Molnár, O., Török, J., Garamszegi, L. Z., Herczeg, G. 2015 European green lizard (*Lacerta viridis*) personalities: Linking behavioural types to ecologically relevant traits at different ontogenetic stages. *Behavioural Processes*. 111, 67-74. doi: 10.1016/j.beproc.2014.11.020. *divided first authorship

Oral presentations and posters that are parts of the thesis

- Horváth, G.,** Martín, J., López, P., Garamszegi, L.Z. and Herczeg, G. 2016: The effect of quantity and quality of diet on male Carpetan rock lizards' (*Iberolacerta cyreni*) activity and risk-taking. Oral presentation. VIII European Conference on Behavioural Biology, 12-15 July 2016., Vienna, Austria. p. 9.
- Horváth, G.,** Martín, J., López, P., Garamszegi, L.Z. and Herczeg, G. 2016: Cold-blooded personalities: Vitamin D and food shortage affects risk-taking behaviour of male Carpetan rock-lizards (*Iberolacerta cyreni*). Oral presentation. 9th Symposium on the Lacertids of the Mediterranean Basin. 20-23 June 2016., Limassol, Cyprus. p. 21.
- Horváth, G.,** Mészáros B., Urszán T., Herczeg, G. 2016. Individual state and behavioural consistency in male European green lizards (*Lacerta viridis*). Oral presentation. 9th Symposium on the Lacertids of the Mediterranean Basin. 20-23 June 2016., Limassol, Cyprus. p. 22.
- Horváth, G.,** Martín, J., López, P., Garamszegi, L.Z., Herczeg, G. 2016: Kiszagolható-e a személyiség? D-vitamin és energiahány hatására hím ibériai hegyigyíkok (*Iberolacerta cyreni*) viselkedési konzisztenciájára. Oral presentation. V. Herpetológiai Előadókör, 7. March 2016., Budapest, Hungary. p. 20.
- Horváth, G.,** Martín, J., López, P., Garamszegi, L.Z., Herczeg, G. D3-vitamin és táplálékmenyiség hatása hím ibériai hegyigyíkok (*Iberolacerta cyreni*) viselkedési konzisztenciájára. Oral presentation. XVIIth Congress of the Hungarian Ethological Society, 27-29 November 2015., Dobogókő, Hungary. p. 27.
- Horváth, G.,** Martín, J., López, P., Garamszegi, L.Z. and Herczeg, G. 2015: The effect of food and vitamin D availability on behavioural consistency of male Carpetan rock-lizards (*Iberolacerta cyreni*). Oral presentation. 18th SEH European Congress of Herpetology, 7-12 September 2015., Wrocław, Poland. p. 48.
- Horváth, G.,** Martín, J., López, P., Garamszegi, L.Z., Bertók, P. and Herczeg, G. 2015: Positive covariation between blood parasite infection and risk-taking in male Carpetan rock-lizards (*Iberolacerta cyreni*). Poster. 18th SEH European Congress of Herpetology, 7-12 September 2015., Wrocław, Poland. p. 130.
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